# ALPINE PHYTOGEOGRAPHY ACROSS THE GREAT BASIN

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ABSTRACT.—Alpine vegetations and floras are compared in two transects across the Intermountain Region. The first extends from the Beartooth Mountains in the central Rocky Mountains to the central Sierra Nevada some 1200 km to the southwest. It includes six mountain ranges. The second transect crosses the Mojave Desert from Olancha Peak in the southern Sierra Nevada to Charleston Peak and thence to San Francisco Peaks in northern Arizona. The largest numbers of arctic-alpine species are in the Beartooth and Ruby mountains, indicating migrations of these species along the Rocky Mountain cordillera. The lowest numbers of arctic-alpine species are in the central and western Great Basin and in the Sierra Nevada. Sørensen's Index of Floristic Similarity was calculated for all possible pairs of the nine alpine areas. There is little correlation of floristic similarity with alpine proximity across the Intermountain Region. Rather, any such correlation seems to be in a north-south direction; this is stronger in the eastern part of the region. Insularity and uniqueness of alpine floras seem to increase toward the western part of the basin. This is probably due to evolution of alpine endemics from preadapted lowland taxa.

The middle-latitude mountains of North America north of Mexico, for simplicity and convenience, may be grouped into four large systems. With few exceptions, the mountains in these systems trend north to south, a fact of considerable importance in the phytogeography of arctic and alpine plants. The four systems are the Appalachians in the eastern part of the continent, the Rocky Mountains, the Cascades-Sierra Nevada, and last, but not least, the Great Basin ranges. The latter three systems dominate the western third of the continent.

In general, the mountain ranges, in their present forms, are younger the closer they are to the Pacific Coast. The Appalachians constitute a very old mountain complex dating from Permian and Triassic times. Much of the large Rocky Mountain system originated in the Laramide Revolution in late Cretaceous and early Paleocene. The oldest basin ranges also rose during the Laramide Orogeny, but most of these ranges, particularly in the west, have been upthrust during a period of time from the Oligocene to the Pleistocene. Additionally, the whole basin floor has been uplifted in the Pleistocene. Orogenic activity continues at present. Even though the Sierran batholith is rather old, the present Sierra Nevada is primarily a product of uplift during the Pliocene and Pleistocene (Axelrod 1962 and pers. comm. 1973; Bateman and Wahrhaftig 1966). Fossil lobed oak leaves at 2850 m in the lower alpine zone on Elephant's Back, south of Carson Pass, lend additional evidence of recent Sierran uplift. The high volcanoes of the Cascades are also of similarly recent age.

## ALPINE ISLANDS IN THE GREAT BASIN

There are some 200 individual mountain ranges within the Great Basin. Most of these trend in a general north to south direction and are separated by broad desert valleys. In the days when mountain ranges were shown on maps by hachures, Dutton described the pattern as similar to an "army of caterpillars marching to Mexico" (Morrison 1965). These basin ranges, with elevations which vary from about 1800 m to over 4300 m, are by no means alike either

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geologically or botanically. Holmgren (1972) divided the region, on the bases of floristics and geology, into four main divisions made up of 16 sections. The mountain ranges within any one section have certain characteristics in common but also there are some rather remarkable ecological differences between mountains within the same section. Holmgren notes that there is greater variation in floristic composition of the alpine zone across the Great Basin from one peak to another than occurs in any other zone. I agree.

For many years, biogeographers working in mountain areas have compared isolated mountain ranges and summits to islands (Wallace 1880, Willis 1922). With increased interest in island biogeography (MacArthur and Wilson 1967), several important papers have appeared which provide quantitative information on the geographical relationships among the biota on isolated montane "islands." Notable among these are those of Hedberg (1970) on the Afroalpine floras, F. Vuilleumier (1970) on páramo avifaunas of the northern Andes, B. S. Vuilleumier (1971) and Simpson (1974) on páramo floras, Brown (1971) on mountaintop mammals in the Great Basin, and, recently, Johnson (1975) on bird species on montane islands in the Great Basin. MacArthur (1972) also carried his theory over to montane islands in the Appalachians in his study of the distributions of thrush species. It is notable that two of these papers (Brown's and Johnson's) are concerned with the islandlike distribution of vertebrates in the Great Basin. Nor have plant geographers ignored the island nature of the Great Basin montane islands (P.V. Wells, pers. comm. July 2, 1968, and, of course, Harper et al. in this symposium).

Both Brown and Johnson have viewed the Great Basin desert "sea" and its montane islands as being bordered on the east and west by large cordilleras, the Rocky Mountains and Sierra Nevada, which they designate as "mainlands" or "continents." The desert sea is open to the south as far as the real sea off Mexico. However, to the north, the desert sea eventually diminishes until it is blocked by the jumbled mountain masses of British Columbia which connect the coastal mountains and the Rockies.

Johnson (1975) used the lower edge of forest-woodland as the perimeter of his islands. This is a real biological boundary. On the other hand, Brown (1971), Harper et al. (this symposium), and I have defined the lower boundaries of the montane islands rather arbitrarily. Harper et al. and Brown have used an elevation of 7500 ft (2286 m) while I have used 9000 ft (2743 m) as an approximation of the extreme lower elevation of alpine plants (Fig. 1). This latter figure is a somewhat liberal estimate of the lower limits of alpine islands in the Intermountain Region, but some alpine sites do exist this low, particularly in cirques. Timberline is usually higher than this and is often very ragged at its upper limits. Upper timberline is frequently used as the boundary between subalpine and alpine vegetation in North America. However, on most mountains of the earth it is not a particularly good boundary, and it is not a good boundary on most American mountains either, including those of the Great Basin. Timberlines almost always exist at much higher elevations than the lowest patches of alpine vegetation. This is often true around glacial valleys, both those with and those without glaciers at the present time. For example, timberline around the Athabaska Glacier in the Canadian Rockies is fully 675 m above the terminus of the glacier, where in the morainal gravels there are a number of arctic-alpine plant species but no trees. The reasons for this ubiquitous phenomenon are rather simple: those factors which define the lower limits of alpine species are not necessarily those which limit the upward distribution of trees.

As Figure 1 indicates, even conservative alpine islands in the Great Basin are much smaller and more isolated from each other than the mountain ranges themselves. But these alpine islands have been both larger and smaller in the past than they are at

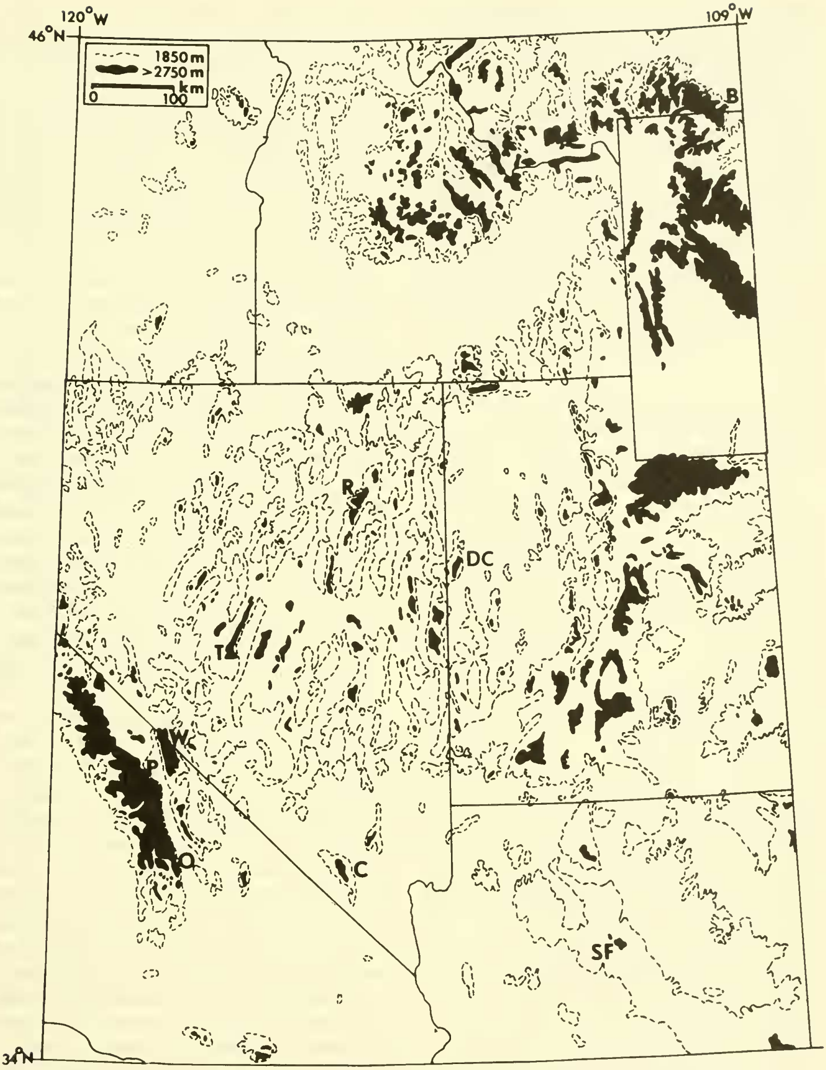

Fig. 1. Map of the Intermountain Region showing, in black, areas above 2750 m in elevation. These represent areas which are wholly or partially "alpine" at the present time. The dashed line at the 1850 m contour is an approximate estimate of what could have been the lower limit of alpine vegetation at full-glacial. Alpine regions used in the northern transect are indicated from left to right by letters: P, Piute Pass (Sierra Nevada); W, Pellisier Flats (White Mts.); T, Toiyabe Mts.; R, Ruby Mts.; DC, Deep Creek Mts.; B, Beartooth Mts. Those in the southern transect are: O, Olancha Pk and two nearby peaks in the southern Sierra Nevada; C, Spring Mts. (Charleston Peak); and SF, San Francisco Peaks.

present. The areas of such islands during glacial and hypsithermal times have had a great deal to do with their present floristics. For example, Simpson (1974) showed that the larger sizes of Andean páramos as they existed at full glacial are more highly and significantly correlated with numbers of plant species per páramo than are the present sizes of each páramo. Also, the distance between páramos at full glacial is almost statistically significant in regard to present-day floristic richness—but the effect of present distance between páramos upon floristic composition is not statistically significant.

Present-day alpine climates on the Great Basin mountains are quite cold during the winter. In this respect, basin alpine climates are probably comparable in winter temperature to alpine areas of the Rocky Mountains and the Sierra, although very few alpine weather data exist to substantiate this. In summer, the basin mountains are far cooler than the desert below. Daytime summer maximum air temperatures are lowest on crests and ridges and nighttime minima are lowest in cirques and canyons; the same relative conditions exist in the Rocky Mountains and Sierra Nevada.

These Great Basin alpine areas are considerably moister than the desert valleys in both winter and summer. However, except for the Ruby Mountains and nearby ranges, they are drier on an annual basis than alpine regions of the Rocky Mountains or the Sierra Nevada because they receive less snow. But they do receive enough snow to form persistent drifts in the lee of cliffs and ridges. It is such drifts that shorten the alpine growing season, keep plants well watered, and allow the growth of alpine plants of certain species. The ranges toward the southwestern part of the basin are relatively drier than the rest because they lie in the most extreme part of the Sierran precipitation shadow. There is a trend toward more winter snow and summer rain in a traverse across the basin in an easterly direction toward the Rocky Mountains. The summer rains in the east are usually in the form of freshening thundershowers, which, I believe, have much to do with the survival so far south of populations of certain arctic species in the Rocky Mountains and eastern basin ranges.

These mountains were much colder and wetter during glacial times up to at least 12,000 years BP. Permanent snow was abundant, and many of the ranges had valley glaciers. These glaciated ranges include the White Mountains, Toiyabe, Santa Rosa, Independence, Jarbidge, East Humboldt, and Ruby Mountains. In the latter range, valley glaciers emerged from the mountains onto the now sagebrush-covered plains. Even far to the south, there were glaciers on the Spring Mountains[2] and San Francisco Peaks. Even though these glaciers were small as compared to glaciers and icefields on the Sierra and in the Rocky Mountains, they did create cirques which are now the refugia for a number of alpine species. The colder, wetter climate also depressed and telescoped vegetational zones and lowered timberlines an estimated 600 to 1200 m (Baker 1970, Loope 1969, Wells and Berger 1969). Even though timberline in itself is neither the only nor the best indicator of alpine conditions, such a depression would have greatly increased the size of basin range alpine islands and decreased the distances between them. This situation would have increased the chances of establishment of arctic-alpine species by long-distance dispersal and, in certain instances, by direct migration over tundralike terrain. Since timberline depression has been variously estimated and since it did undoubtedly vary from one part of the Basin to another, I have compromised by showing in Figure 1

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[2] In botanical literature, the Spring Mountains are frequently, but incorrectly, called the "Charleston Mountains" due mainly to the title of Clokey's (1951) flora of the central portion of the range dominated by Charleston Peak.

what a 900 m depression would do to the sizes and proximity of alpine islands and continents at full glacial.

Not only have the alpine islands been larger in the past, they have also been smaller. During the hypsithermal, about 7500 to 4500 years BP, timberlines of *Pinus longaeva* in the White Mountains and the Snake Range advanced upward to a level about 100 to 150 m above where they now stand (LaMarche and Mooney 1967). Such a long period of warmth and aridity could have eradicated some alpine species by forest shading or by eliminating their snowy refugia on the higher peaks.

The hard rock geological history of the Basin Ranges is a complex and varied one. I shall not go into it here. Suffice to say that sedimentary rocks, and thus calcareous substrata, are more abundant in the eastern ranges while the western rocks tend to be igneous or metamorphic, and yet with some dolomites and other calcareous types. To many alpine plants, the chemical natures of these different kinds of substrates are all-important in marginal habitats.

## Alpine Vegetations and Floras

In any study of vegetation and flora, it is important to distinguish clearly between "origin" and "maintenance" of each. Origin is very difficult to pinpoint, and particularly so with alpine floras because they leave almost no macrofossils. However, the presence of diploids in widespread polyploid arctic-alpine species may play the role of "cytological fossils." The origin of a particular flora on any mountaintop is the result of the interaction of many factors: past geologic events, past climates, migrations of each species, polyploidy, evolution, and even man's activities. Hypotheses are numerous; answers are few.

While maintenance of an alpine flora and its vegetation is somewhat easier to understand, there is still much work involved. One must measure the characteristics of ›oth the physical and biological aspects of environment, preferably along meso- and microtopographic gradients throughout the year (Billings 1973). Also, it is necessary to know the tolerance ranges of plant populations in any particular place. This requires many field measurements and much laboratory experimentation under controlled conditions. We have made only a beginning in understanding maintenance of some alpine plant species. Such studies require the interaction of many people; they are not one-person jobs.

## Alpine Vegetations

In trying to reach at least a partial understanding of alpine phytogeography and ecology in the Great Basin, it is helpful to start by describing alpine vegetations as they now exist from the Rocky Mountains across the basin ranges to the Sierra Nevada. A good approach is to look at these vegetations along a northeast to southwest transect from the Beartooth Mountains on the Montana-Wyoming line to the central Sierra Nevada. Such a transect crosses many of the basin ranges, but of particular interest are the Ruby Mountains, the Toiyabe Range, and the White Mountains. These represent the eastern, central, and western basin ranges, respectively.

Quantitative analyses of alpine vegetation have been made in the Beartooth Mountains (Johnson and Billings 1962), the northern Ruby Mountains (Loope 1969), the White Mountains (Mooney 1973), and the central Sierra Nevada (Chabot and Billings 1972). I do not know of any quantitative alpine vegetational data from the Toiyabe or Toquima Ranges; perhaps there are some. The floristic information and photographs in Linsdale et al. (1952) are of some help, as are personal qualitative observations which I made in 1949.

Space does not allow the presentation of those long tables of vegetational composition which do exist; one simply can refer to the publications listed above. However, the alpine vegetation of the Beartooth Mountains is typically Rocky Mountain alpine with large expanses of alpine tundra in the true sense: *Geum rossii* turf in mesic sites, *Deschampsia caespitosa* meadow in moist sites, and *Carex scopulorum* in wet bogs. The crests and ridges are occupied by rather dense stands of cushion and rosette plants with *Silene acaulis*, *Carex elynoides*, and many other species dominating. Early and late snowbeds are abundant and have characteristic species surrounding them.

Alpine vegetation in the Ruby Mountains lacks the broad expanses of tundra characteristic of the Beartooth. However, south of Lake Peak along the divide there is fairly extensive tundra at elevations from 3140 m to 3300 m. This alpine vegetation is characterized by *Silene acaulis* and *Carex pulvinata*. Similar alpine vegetation exists at the same elevation on the north slope of Wines Peak, with *Geum rossii* and *Silene acaulis* being the dominants. *Carex scopulorum* grows in dense stands around alpine ponds. Some of the best-developed alpine vegetation in the Rubies is in the cirque floors. In Island Lake cirque, the vegetation is dominated mainly by *Erigeron peregrinus*, *Salix arctica*, *Caltha leptosepala*, *Geum rossii*, *Sibbaldia procumbens*, and *Polygonum bistortoides*. *Oxyria digyna* is common on rocky, moist sites, particularly around snowbanks. One is struck with the remarkable similarity in species composition and site characteristics to the alpine vegetation of the Beartooth some 700 km to the northeast. Essentially, the alpine vegetation of the Ruby Mountains is a small, only slightly attenuated, isolated example of Rocky Mountain alpine vegetation.

In strong contrast, the alpine vegetation of the Toiyabe Range, only 250 km southwest of the Rubies, apparently bears little resemblance to that of the northern Rubies or to that of the Rocky Mountains. It seems to be an open, rocky vegetation with a few scattered alpine grasses such as *Trisetum spicatum* and various species of *Draba* and *Eriogonum*, some of which are endemic. There is not the great variety of alpine vegetation types which one sees in the Rocky Mountains. More vegetational work is needed in the small and little-known alpine areas of the central Great Basin; further study may change our ideas of these regions of what might be termed alpine desert.

Another 150 km farther southwest is the long and high massif of the White Mountains. In contrast to the Toiyabe and Toquima Ranges, this has been rather intensively studied environmentally, vegetationally, and floristically. The alpine vegetation has been well-described by Mooney et al. (1962), Mitchell et al. (1966), and Mooney (1973). Over most of the extensive alpine area in the White Mountains, the vegetation is extremely sparse; Mooney (1973) reports a plant cover of only 1.5 percent at 4175 m on the side of White Mountain Peak. Mitchell et al. (1966) say that vegetational cover on windy, gravelly flats on Pellisier Flats, an area of 21 km$^2$ near the north end of the range, rarely exceeds 15 percent. However, on seepage banks and meltwater runs, vegetational cover ranges from 10 to 95 percent. Pellisier Flats at 4100 to 4430 m has active frost polygons and miniature solifluction steps reminiscent of the Beartooth Plateau. The most striking vegetational feature of the White Mountains, however, is the sharp distinction in vegetation and flora between the dolomite barrens and granite or quartzite fell-fields. The dolomite barrens are very desertlike and, although in places they may have vegetational cover up to 12 percent, in other places there are almost no plants. *Phlox covillei* and *Eriogonum gracilipes* are characteristic species on the dolomite. A granite fell-field at 3870 m had a vegetational cover of 50 percent and was dominated by *Trifolium monoense* and *Koeleria cristata*; the first is essentially endemic to the White Mountains and the second is a cosmopolitan species. The alpine vegetation of the White Mountains is decidedly unlike that of the Rubies—but both are Basin ranges.

There have been several vegetational studies made on alpine vegetation in the

Sierra Nevada. These vary considerably between the northern end of the range and the southern, where the peaks are higher and the climate drier. Only 48 km southwest of the White Mountain crest and within sight of it, is Piute Pass at 3540 m on the Sierran white granite. Here, Chabot and Billings (1972) found the low alpine vegetation covering less than 30 percent of the rocky ground and characterized by *Lupinus breweri*, *Antennaria rosea*, and *Carex helleri*. Other common Sierran alpine species in similar locations on nearby peaks and ridges are *Phlox caespitosa*, *Penstemon davidsonii*, *Ivesia pygmaea*, and *Draba lemmonii*. At higher elevations, *Oxyria digyna*, *Polemonium eximium*, and *Hulsea algida* are constant members of the alpine vegetation usually on scree slopes. The most luxuriant vegetation near here is along snowbank meltwater brooks where *Dodecatheon jeffreyi*, *Lewisia pygmaea*, and *Sedum rosea* occur. On very thin granitic soils which dry out after snowmelt, only *Calyptridium umbellatum*, the dwarf *Koenigia*-like endemic *Polygonum minimum*, and one or two other species can exist. There is a great difference in alpine vegetation here, not only from that of the Beartooth but also from that of the White Mountains on the near horizon.

## Alpine Floras

While there are a few floras for whole mountain ranges between the Rocky Mountains and the Sierra, e.g., Lloyd and Mitchell (1973) for the White Mountains, the main sources of alpine floras per se appear to be journal papers or theses. Referring again to Figure 1, I have assembled at least tentative figures on the numbers of alpine species for the same NE-SW transect along which the trend in alpine vegetation has been described. These figures will certainly be changed with additional collecting and publication, particularly of more volumes of Cronquist et al. Intermountain Flora and Howell's proposed Sierran Flora. The sources are the Beartooth Mountains (Johnson and Billings 1962), the Deep Creek Mountains (McMillan 1948), the Ruby Mountains (Loope 1969), the Toiyabe Range (Linsdale et al. 1952), the White Mountains (Mitchell et al. 1966), and the central Sierra Nevada (Chabot and Billings 1972). Additionally, I have included floristic data from a series of three isolated alpine areas across the southern desert region. From west to east these are Olancha Peak and its neighbors in the Sierra Nevada (Howell 1951), the Spring Mountains (Clokey 1951), and San Francisco Peaks (Little 1941).

Many alpine plant species also occur in the Arctic. As a basis for whether or not our species do, I have checked each against Polunin's (1959) Circumpolar Arctic Flora. Species which are not arctic-alpine may be endemic to a continental region of the middle-latitudes or to the mountain range itself or its near neighbors. While we need much more information on both scores, the absolute figures on arctic and endemic species in each small alpine area can tell us something about migrations into an area and possibly about the evolution of new species after such migrations from afar or from the arid regions below. Nor should we forget that some endemic species may be relicts or that some widespread arctic-alpine species may have become extinct during xerothermic times, or that some may never have reached certain alpine areas because of lack of adaptation for long-distance dispersal.

The upper part of Table 1 (the Beartooth-Sierra transect) illustrates immediately that there are many alpine species in the central Rocky Mountains that also occur in the Arctic. In the Beartooth Mountains, 91 out of 194, or almost half the alpine flora, also occurs in the Arctic. This is in contrast to the 24 arctic-alpine species in the Deep Creeks and 47 in the Rubies; but these are somewhat smaller ranges. The composition of the alpine floras of both of the latter ranges, however, is very much a Rocky Mountain-type flora. In contrast, west of the Ruby Mountains there is a dramatic drop in not only the total numbers of alpine species in the Toiyabe, the White Mountains, and the Sierra Nevada, but also in the number of arctic-alpine taxa present. The arctic-alpine element consists, in these ranges, mostly of such easily dispersed, ubiquitous species as *Oxyria digyna*, *Trisetum spicatum*, *Cystopteris fragilis*, and *Androsace septentrionalis*. Even common species such as *Silene acaulis* are missing, not to mention relatively rare taxa such as *Koenigia islandica*, *Saxifraga flagellaris*, or *Phippsia algida*. Widespread arctic-alpine species such as *Silene acaulis*, *Polygonum viviparum*, and *Salix arctica* reach their western limits in the Great Basin in the Ruby Mountains and do not reappear in the Sierra Nevada (Loope 1969). Since these species are not that particular in their environmental requirements (there are apparent places in the Sierra Nevada where they could grow), they either must be poorly adapted to long-distance dispersal or there is or has been an advantage to migrating north or south along the old tried and true Rocky Mountain pathway. Those arctic-alpine species in the Sierra Nevada most likely came down from the north in glacial or cooler times during the Pleistocene. Migration across the Great Basin appears to have been a chancy thing even at full-glacial. Only species with propagules easily dispersed by wind or birds appear to have made it to the central Great Basin mountains. Even after possible establishment, some alpine species may have become extinct on the Great Basin peaks in dryer, postglacial times. Axelrod (1976) also suggests extinctions of moist environment subalpine conifers and alpine species in the Great Basin during these xerothermic episodes. I believe that extended post-glacial dry periods also could have eliminated such dry-site arctic-alpine species as *Silene acaulis* and *Saxifraga cespitosa* in the Sierra Nevada where they do not occur today. This suggestion, of course, must assume that these species migrated into the Sierra Nevada, probably from the north, during favorable Pleistocene times.

Looking at the southern transect in Table 1, the same dearth of arctic species is apparent in the Olancha Peak group at the southern end of the Sierra and particularly so on Charleston Peak in the isolated Spring Mountains where only 9 arctic species are known to occur. In contrast, only

TABLE 1. Total numbers of true alpine species and those which also occur in the Arctic (arctic-alpine) in two transects across the Intermountain Region. Data from several sources.

| Location | Total No. of Alpine Species | No. of Arctic-Alpine Species | Percent of Arctic-Alpine Species |
|---|---|---|---|
| NORTHERN TRANSECT | | | |
| Beartooth Mts. | 194 | 91 | 47 |
| Deep Creek Mts. | 80 | 24 | 30 |
| Ruby Mts. | 189 | 47 | 25 |
| Toiyabe Range | 48 | 11 | 23 |
| White Mts. (Pellisier Flats) | 48 | 10 | 21 |
| Piute Pass (Sierra) | 41 | 4 | 10 |
| SOUTHERN TRANSECT | | | |
| Olancha Pk., etc. (Sierra) | 102 | 13 | 13 |
| Spring Mts. | 39 | 9 | 23 |
| San Francisco Pks. | 49 | 19 | 39 |

350 km to the southeast, the San Francisco Peaks have at least 19 arctic species in spite of their isolation. Also, there is a distinct Rocky Mountain cast to their alpine flora. A possible pathway for migration into this Pleistocene volcanic mountain may have been at full-glacial through the Arizona White Mountains to the southeast, or the source may have been through the Wasatch Plateau to the north. Again, we come to the origin versus maintenance problem: these arctic species would not remain in the volcanic cinders or the glacial cirques of this isolated mountain, no matter how they got there, except for the summer thundershowers reinforcing the winter snows as a source of water.

Much more poorly known are the endemics of all of the above mountain ranges. Alpine endemics are much less common in the central Rocky Mountains than in the Sierra Nevada. This may be due to lack of isolation along the Rocky Mountain system. The Sierra Nevada as a whole has many endemic alpine species but I do not know how many of these may be narrow endemics restricted to the two small regions listed in Table 1. The White Mountains have several alpine endemics, and since they cover so much less area than the Sierra Nevada, the chances of these being narrow endemics are better than in the latter range. The same fact holds true for the isolated ranges of the central Great Basin. Some of these latter endemics may also prove not to be so narrow, except edaphically, upon further exploration. For example, consider *Primula nevadensis* (Holmgren 1967). The isolated Spring Mountains, with an alpine flora of only 39 species at most (some of these are probably subalpine), has at least 4 endemic alpine species. It seems that alpine endemism tends to be more common in relation to total alpine floras on isolated, nonvolcanic peaks and ranges in the southwestern part of the Intermountain Region; this includes the southern part of the Sierra Nevada. The real answer to the question of distribution of endemics lies in more collecting in alpine environments and systematic description of the taxa.

One way of comparing alpine floras is to use Sørensen's (1948) Index of Floristic Similarity. This is expressed as:

$$IS_s = \frac{c}{1/2\ (A+B)} \times 100$$

where, $IS_s$ = Sørensen's Index of Similarity
c = number of species held in common by two alpine areas
A = total number of alpine species in Region A
B = total number of alpine species in Region B

Taking the available alpine floristic data from each of the nine alpine areas on both transects, I calculated Sørensen's Indices for each possible comparison. These indices are presented as percentage values in Table 2. Also, in the same table, direct distances in km between the alpine areas are shown. When the Indices of Similarity are plotted against distance for each pair of alpine areas, the result is a great deal of scatter in the points. There is little evidence of inverse correlation of floristic similarity between these alpine regions with distance. Out of 36 possible combinations, only 4 show indices above 30 percent combined with distances below 200 km. These are the Deep Creek—Ruby Mountains in the east-central Great Basin and Pellisier Flats-Olancha Peak, Pellisier Flats-Piute Pass, and Piute Pass-Olancha Peak, all in the Sierra Nevada-White Mountain complex at the extreme southwestern edge of the Great Basin. Two others had indices almost equally as high but at distances between 500 and 700 km; these are the Deep Creek Mountains—San Francisco Mountains and Beartooth-Ruby Mountains combinations. The most distant range, the Beartooth, has higher indices of similarity with the Ruby Mountains, Deep Creek Mountains, and San Francisco

Mountains alpine floras at distances of 650 to 1100 km than any of these latter ranges have with the Spring Mountains at distances less than 500 km. The distant Rocky Mountains alpine flora as exemplified by that of the Beartooth has as great or greater an influence on those of most of the Great Basin mountain ranges than does that of the much closer Sierra Nevada. There is even a greater (two to three times) similarity between the alpine floras of San Francisco Mountains and the Deep Creek Mountains at a distance of 531 km than there is between the Deep Creek flora and those of the Sierra Nevada and White Mountains, which are equally distant from the Deep Creek Mountains.

The rather low indices of similarity indicate at least one fact rather clearly: these Intermountain Region alpine areas are very much like newly isolated islands. This is well illustrated along the southern transect from Olancha Peak to Charleston Peak to San Francisco Peaks. With the two gaps being only 225 and 378 km across, respectively, the indices of similarity are only 13 and 14 percent. The Olancha Peak group is clearly Sierran, Charleston Peak is unique, and San Francisco Peaks show strong relationships to the Rocky Mountains and

TABLE 2. Sørensen's indices of floristic similarity (in percent) between alpine floras for all combinations of alpine areas in both transects. Numbers in parentheses are distances (in km) between the alpine regions. Also, see map in Fig. 1.

Northern Transect

| | Beartooth | Deep Creeks | Ruby Mts. | Toiyabe Range | Pellisier Flats (White Mts.) | Piute Pass (Sierra) |
|---|---|---|---|---|---|---|
| Beartooth | – | 24% | 33% | 14% | 14% | 9% |
| Deep Creeks | (676) | – | 39% | 22% | 19% | 10% |
| Ruby Mts. | (692) | (153) | – | 20% | 14% | 11% |
| Toiyabe Range | (917) | (322) | (257) | – | 21% | 16% |
| Pellisier Flats (White Mts.) | (1102) | (451) | (418) | (145) | – | 34% |
| Piute Pass (Sierra) | (1167) | (515) | (483) | (217) | (72) | – |
| Olancha Pk. Group (Sierra) | (1223) | (547) | (539) | (290) | (169) | (129) |
| Spring Mts. | (1110) | (434) | (475) | (325) | (298) | (306) |
| San Francisco Pks. | (1086) | (531) | (668) | (636) | (660) | (668) |

Southern Transect

| | Olancha Pk. Group (Sierra) | Spring Mts. | San Francisco Pks. |
|---|---|---|---|
| Beartooth | 14% | 8% | 23% |
| Deep Creeks | 15% | 13% | 31% |
| Ruby Mts. | 14% | 8% | 19% |
| Toiyabe Range | 13% | 18% | 21% |
| Pellisier Flats (White Mts.) | 36% | 16% | 19% |
| Piute Pass (Sierra) | 32% | 10% | 4% |
| Olancha Pk. Group (Sierra) | – | 13% | 13% |
| Spring Mts. | (225) | – | 14% |
| San Francisco Pks. | (603) | (378) | – |

mountain ranges far to the north. These affinities of the San Francisco Peaks alpine flora have also been noted by Moore (1965).

After examining the existing floristic data on alpine species across the Great Basin, it is tempting to delineate some alpine phytogeographic boundaries. Certainly, there is a sharp boundary just west of the Ruby Mountains separating Rocky Mountain types of vegetation and flora from that of the Great Basin. Where this boundary goes to the south, I am not prepared to say. Certainly, it would appear to be west of the Snake Range and perhaps west of the Grant Range; but this is tentative and probably premature. It obviously lies between San Francisco Peaks and the Spring Mountains.

Another alpine phytogeographic boundary lies between the White Mountains and the Sierra Nevada and winds north in sinuous curves until it divides the Carson Range on the west from the Pine Nut Range on the east; but several species pay no attention to such an imaginary line and go their way from the Sierra Nevada into the altered andesites of the Virginia Range (Billings 1950) and the nevé cirques of the Pine Nut and Wassuk Ranges (Billings 1954). Again, if edaphic or moisture conditions are right,some species can get to seemingly inhospitable mountain ranges and stay there perhaps by infraspecific physiological adaptations (i.e., ecotypes).

## Possible Origins of Intermountain Alpine Floras

Alpine floras originate in all mountains by migration and/or evolution; the mountains of the Intermountain Region are no exception. Refugia, both glacial and interglacial, are also important. As Figure 1 shows, and as Simpson (1974) has demonstrated for the páramos, successful long-distance dispersal is greatly influenced by the sizes and proximity of alpine islands. Such islands were obviously larger and closer during glacial and cooler times. From distributional evidence, only a relatively few arctic-alpine species appear to be able to migrate far: *Oxyria digyna*, *Saxifraga cespitosa*, *Trisetum spicatum*, and *Cystopteris fragilis*, for example. Therefore, it is advantageous for ancestral species to be nearby when mountains arise or new alpine areas come into existence by climatic causes. It also seems to be advantageous to be on a north-south migration route such as the old Rocky Mountains, or even the much younger Cascade-Sierran system. The ability to evolve rapidly by adaptive radiation is also advantageous, as for example, in the genus *Espeletia* in the Andean páramos.

Such plasticity, plus pure luck in being near refugia, either edaphic or microclimatic, also helps. Interglacial refugia are fully as important as glacial refugia. Such interglacial refugia can be mountaintops such as Mount Washington, New Hampshire, altered volcanic rocks as in the Virginia Range of western Nevada (Billings 1950), alpine snowbanks, and the moist, cool floors of impervious cirques (Loope 1969). Loope ascribes the presence of many arctic species in the Ruby Mountains today to its nonporous (moist) cirque floors as compared to the porous, dry cirque floors of the Jarbidge Mountains to the north and those of the Snake and Schell Creek ranges to the south.

There are other sources of alpine floras in the Intermountain Region. These are the surrounding desert floras as suggested long ago by Went (1948) and experimentally investigated by Klikoff (1966) and by Chabot and Billings (1972) for the Sierra Nevada. The principal findings reported in the latter paper would apply almost as well to the mountain ranges of the Great Basin, provided there are suitable sites for such migration and evolution, and providing there are species and genera of sufficient genetic plasticity near at hand. The derivation of a new alpine flora from a desert or semidesert flora is aided by the following:

a. preadaptation of winter annuals and perennials in regard to physiology and morphology,

b. the ability to migrate upward during favorable climatic periods into new but not altogether dissimilar environments,
c. selection for metabolism at low summer temperatures,
d. selection for low temperature starch degradation and sugar translocation at night,
e. selection of populations and ecotypes which acclimate metabolically rapidly and ideally, and
f. selection for flowering and seed-set in short, dry cool growing seasons.

These have been elaborated in detail by Billings (1974).

There is every reason to believe that such upward evolution of new "alpine-desert" taxa is taking place in the Great Basin. But the rate may be slower than in the Sierra Nevada due to a smaller preadapted flora and also due to the drier and less snow-protected environments on the peaks. In such a case, there could be a trend toward edaphic endemism because other kinds of habitat diversity are in relatively short supply. Such upward mobility and long-distance dispersal over great distances in a north-south direction seem to be the principal sources of the alpine floras of these isolated montane islands in the central Great Basin.

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